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HEREDITY AND ORGANIC SYMMETRY IN ARMADILLO QUADRUPLETS.

II. MODE OF INHERITANCE OF DOUBLE SCUTES AND A DIS- CUSSION OF ORGANIC SYMMETRY.

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A. GENERAL STATEMENT.

This paper is in continuation of a study published under the same general title in July, 1915. In that paper the inheritance and distribution among quadruplets of more or less extensive band anomalies were dealt with. All anomalies involving the presence of two or more consecutive double scutes either in mother or in one or more offspring of a polyembryonic set were considered as *band* anomalies. There remained numerous cases of inherited anomalies so minute as to involve only isolated double scutes in parent and in offspring. A detailed study of the inheritance and of the symmetrical or asymmetrical distribution of these double scutes among the fetuses of quadruplet sets forms the subject matter of the present contribution.

In order to have a compact and truly homogeneous group to work with, I have decided to confine my study to collections *C* and *K*, omitting several small collections, the data of which are not so complete. In the *C* and *K* collection there are 140 sets of quadruplets which are sufficiently advanced to show every detail of the scute pattern. The shells of the mothers of all these sets are preserved and have been carefully scutinized for anomalies. Such shells as were badly worn or damaged had to be excluded from the present study together with the associated offspring. A study of 140 sets should reveal the conditions typical for the species, since we have a collection of 700 individuals. Of the 140 sets of quadruplets 73 are female and 67 male. This discrepancy between the sexes is due to two circumstances, first that three sets of fetuses, in which the sex was obviously male, were too small to count, the mothers in all cases being normal,

and second that two sets of offspring, all normal and males, were discarded because the shell of the mother in each case was badly damaged. If these five sets of male quadruplets be added the count would be practically even so far as sex goes, 73 females and 72 males. Other collections, moreover, have shown equal numbers of male and female sets of quadruplets.

I. *Three Categories of Offspring.*

A survey of the 140 sets of quadruplets reveals that there are three well-defined classes:

(a) Those in which both mother and offspring have anomalies. Of these there are 56 sets, 29 female and 27 male.

(b) Those in which the mother is normal but the offspring have anomalies. Of these there are 41 sets, of which 22 are female and 19 male.

(c) Those in which both mother and offspring are normal. Of these there are 43 sets, of which 22 are female and 21 male.

Unless the character in question is strongly inherited as a dominant we would expect to find a fourth class composed of sets in which the mother has an anomaly but all offspring are normal. Only one such case occurs, and this is a doubtful one in which the anomaly of the mother is a double scute that may be due to the fusion of two scutes after a local injury. This doubtful case has been included in class (c). Another case that I at first thought was in this fourth class was found on examination to belong to class (a), for one of the fetuses had a double scute in the last scapular band which had been overlooked in the counts because we were dealing only with the regular bands. The facts of this case will be clear from an examination of Set C 65 (bottom of p. 187).

The mode of inheritance of these anomalies does not appear to be typically Mendelian, for, if the character is a dominant, with the normal condition the recessive, we would expect a considerable number of anomalous individuals to be heterozygous for the character and to produce equal numbers of germ cells with the anomaly factor and without it; so that on the basis of chance mating we should often get normal offspring from the mating of two heterozygous anomalous parents or from one heterozygous

anomalous parent pairing with a normal parent. That we do not find this condition means that we have evidently a non-Mendelian result due probably to factor segregation among the quadruplets, a process that must evidently take place in order to produce sets in which some individuals are anomalous and some are normal. This segregation must also affect the germ cells, so that an individual that has an anomaly has also germ cells of only one kind and these homozygous for the anomaly factor. The same kind of mechanism that quite evidently segregates the somatic anomaly factor must also be conceived of as responsible for a segregation of the germinal anomaly factor. The results do not appear to bear any other interpretation. Further discussion of this point follows the presentation of data.

Since these anomalies are invariably inherited when present in the mother we are driven to the conclusion that all these sets in class (*b*), which have anomalies, but whose mothers are normal, must have inherited their anomalies from the father. Furthermore, it is equally obvious that a considerable proportion of those sets in class (*a*) must have anomalous fathers as well as anomalous mothers. Thus class (*a*) is heterogeneous in that it is composed of sets inheriting from both parents, on the one hand, and from the mother alone, on the other.

A calculation may readily be made of the relative sizes of the various classes of offspring that should result if chance mating occurs between anomalous and normal individuals. It will be noted that 56 of the 140 mothers (or 40 per cent.) have anomalies. Again 115 individual female offspring, or 39+ per cent. and 111 individual male offspring or 41+ per cent., have anomalies. So we may be safe then in assuming that 40 per cent. of the individuals of the species have anomalies and 60 per cent. have none. If 140 chance matings on this basis occur we should expect the following classes:

- (*a*) 16 per cent. or 22.4 with both parents anomalous.
- (*a'*) 24 per cent. or 33.6 with mother only anomalous.
- (*b*) 24 per cent. or 33.6 with father only anomalous.
- (*c*) 36 per cent. or 50.4 with neither parent anomalous.

The sum of classes (*a*) and (*a'*) is 56, which is exactly the number of sets in the observed class (*a*).

The observed class (*b*), 41 sets, is several sets in excess of expectation, but not enough to seriously effect the theory of breeding proposed. The observed class (*c*), 43 sets, is several sets too low, but it is very probable that the five discarded male sets referred to above belong to this category. On the whole, then, the observed and theoretical proportions of the categories of offspring are as close as could be expected in 140 matings, and this fact supports the general statement as to the modes of inheritance of these anomalies stated above.

2. The Genetic Relation Between Scute and Band Anomalies.

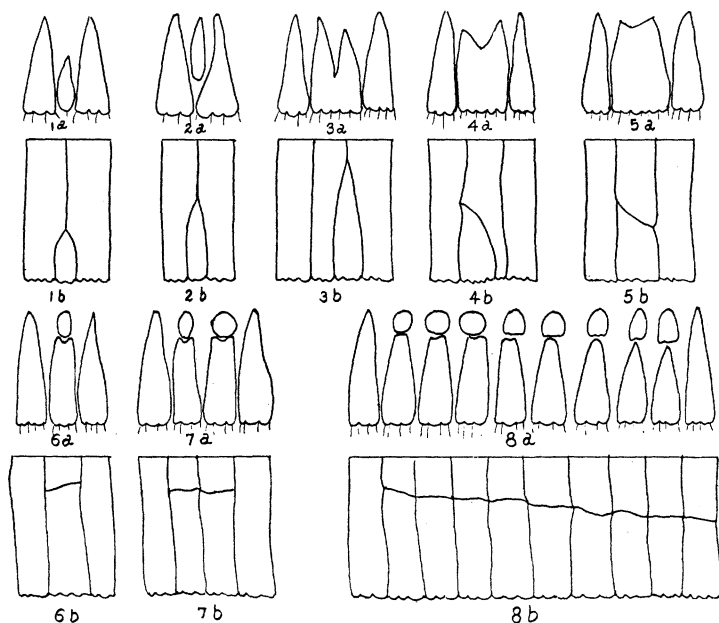
There is a very intimate genetic relationship between band and scute anomalies, as was brought out in the previous paper (Newman, '15). Sometimes a band anomaly is inherited as such in some offspring of a set, and as a scute anomaly in others; and the localization in all cases is so exact that there can be no doubt about the genetic equivalence of the two anomaly phases.

In Figs. 1-8 is arranged a series of drawings of scute anomalies leading up to band anomalies. The transition is more readily made out from the conditions in the bony plates underlying the scutes. Fig. 1*a* represents the appearance from the exterior where only the scute is visible; Fig. 1*b* shows the underlying plate condition. Similarly with Figs. 2*a* and 2*b*, etc. In Fig. 6, *a* and *b*, we see that the more fundamental anomaly is a transverse splitting of the bony plate involving only one unit. Fig. 7, *a* and *b*, constitutes an incipient or minimal double band, while Fig. 8, *a* and *b*, represents a band doubling of moderate extent involving six scutes. Such band doublings may involve more than half of a band or there may be extensive doubled regions separated by single or undoubled regions.

Since the bony plates are fully laid down only during post-embryonic life, it is impossible to study these structures in the fetuses that are taken from the uteri of the mothers; but the scute condition, for one who has made a study of the subject, serves as a very definite index of the condition of the bony plate; and the scutes are well defined long before birth. For example, whenever a scute is found with a deep notch above dividing the scute into two nearly equal cusps (as in Fig. 3*a*), one can be sure that the

bony condition will be like that in *3b*. Similarly when the notch is shallow as in *5a*, we might expect the bony condition to be as in *5b*.

It is an open question as to which doubling is more fundamental, that of the dermal plate or that of the horny scute. Ontogenetically the scute is the older structure, but I am inclined to look upon the two structures as phylogenetically coeval, for we apparently have in the armadillo a case of the persistence in a



FIGS. 1-8.

mammal of the ancestral reptilian epidermal scale with its dermal bony core. The hair group that centers about the scute is presumably of more recent origin.

I look upon scute and plate doubling as cases of local budding of normally single primordia, not unlike the division of scutes and plates in the carapace of modern tortoises, a phenomenon that has received considerable attention (Newman, '05, and Coker, '10). The physiological basis of this budding may be a localized lowering of the rate of growth during scute development. If we had a solution of the problem of budding or division

in this instance we would have a solution of the general problem of division that appears everywhere in the field of biology.

Since the inheritance and distribution of double bands was dealt with in detail in the earlier paper of this series it will not be necessary to refer further to these results. It may be of interest, however, to compare the facts as to symmetry phenomena in the two classes of anomaly. Band anomalies are much less numerous than anomalies of single scutes, but they exhibit the same mirror-image phenomena and symmetry reversals that are so frequently seen for double scutes. For details of these phenomena the reader is referred to the published account (Newman, '15).

The present study deals solely with scute anomalies, double or split scutes of the various types shown in Figs. 1 to 6.

3. *Frequency and Distribution of Scute Anomalies.*

In the present collections (*C* and *K*) there are 700 individuals composed of 140 sets of quadruplets and their mothers. These should constitute for statistical purposes a reasonably adequate sample of the species.

In the earlier paper of this series (Newman, '15) 23 sets that showed band anomalies in one or more members of a set were dealt with. Many of the individuals (40 in all) had scute anomalies, some with and some without accompanying band anomalies. The remaining 117 sets (585 individuals) treated in this paper contain 199 individuals with double scutes. Whether we figure on the basis of the entire collection or upon the 117 sets dealt with in the present paper we find that 34+ per cent. of all individuals have scute anomalies. Add to this 32 (4+ per cent.) individuals that have only band anomalies and we find that about 39 per cent. of all individuals have either band or scute anomalies or both, which is very close to the 40 per cent. arrived at earlier in this paper. Scute anomalies are, however, about eight times as numerous as band anomalies and furnish better material for statistical study.

4. *Sex Distribution of Anomalies.*

Exclusive of the mothers, exactly 40 per cent. of which have anomalies, 22 females and 12 males have band anomalies, and

87 females and 100 males have scute anomalies. There appears therefore to be a somewhat pronounced tendency toward band anomalies as against scute anomalies in females and the reverse in males. In a collection of this size, however, these differences may not be significant.

5. *Distribution of Scute Anomalies as to Bands.*

In the earlier paper of this series it was shown that the band anomalies are largely confined to the first two bands: 86 per cent. in band 1, 8 per cent. in band 2, and the rest scattered; none occurring in bands 5 or 6, which are in the middle of the banded region, or in band 9. The reason given for this state of affairs is that band doubling is normal for the scapular and pelvic regions and that the bands nearest the scapular and pelvic shields are naturally more like these regions than are those farther removed from them.

A somewhat similar condition, though less pronounced, is brought out by a census of double scutes according to bands:

Band 1	has	double	scutes	67	times.
Band 2	"	"	"	40	"
Band 3	"	"	"	40	"
Band 4	"	"	"	34	"
Band 5	"	"	"	9	"
Band 6	"	"	"	27	"
Band 7	"	"	"	34	"
Band 8	"	"	"	29	"
Band 9	"	"	"	9	"

It is significant that double scutes, like double bands, occur most frequently in the first three bands and least frequently in bands 5 and 6 and 9, where band anomalies were entirely absent. Bands 5 and 6 are farthest from the scapular and pelvic regions where doubling is the normal condition. Band 9 is really not a free band at all, but only partially free at the margins; hence it may be left out of consideration. It is really out of the series of bands and should be included in the pelvic shield, but, out of deference to the time honored name "nine-banded armadillo," I have treated it as the ninth band.

I interpret the figures for both double bands and double scutes as I formerly interpreted similar facts brought out by a study of supernumerary scutes in the carapace of tortoises. These supernumerary scutes were viewed as atavistic variations or vestiges of a condition largely outgrown by the species. These anomalies occur most frequently at the posterior end of the carapace and progressively less frequently as one goes toward the anterior end, except that there is a slight increase just at the anterior end. The hypothesis was ventured that the more frequent the regional occurrence of an archaic character the more recent has been the racial suppression of these characters in that region. There has evidently been an antero-posterior orthogenetic loss of scutes in the tortoise carapace beginning at or near the anterior end and ending with the posterior end.

Now in the armadillo I believe that the more generalized and less regular parts of the carapace, the scapular and pelvic shield, represent phylogenetically an older condition than does the banded region. In support of this contention I cite the fact that the extinct giant armadillo, *Glyptodon*, had a solid non-banded carapace. The first banding began in one or two bands at about the middle of the carapace, where bands 5 and 6 are, and proceeded posteriorly and anteriorly. Progress anteriorly in the direction of more bands is probably occurring now, as may be judged by two facts, first that it is not uncommon to find a part of the last scute row of the scapular shield separated as a band, and second that there are not infrequently local fusions between parts of the first band and the scapular shield. On this hypothesis band 1 is the newest band phylogenetically and shows more resemblance to the scapular shield than do other bands, both in band doubling and in scute doubling. Band 2 is much less affected with these anomalies than is band 1, but more so than any other band. Moreover, bands 5 and 6, which are phylogenetically the oldest bands, show the fewest recurrences of irregular conditions. Scute doublings are viewed as incipient or vestigial band doublings and we find many more of these vestigial anomalies in the banded region than fully developed ones.

In the tortoises the orthogenetic progress in carapace simpli-

fication has proceeded antero-posteriorly and in this single direction. In the armadillo banding has proceeded both ways from the middle. Various armadillo species today exhibit all the way from one to twelve bands, a fact that supports the idea that in our species there has been a gradual increase in the number of bands.

B. PRESENTATION OF DATA CONCERNING THE INHERITANCE AND DISTRIBUTION AMONG QUADRUPLETS OF DOUBLE SCUTES.

The following tabulation gives all of the facts concerning double scutes, except those brought out in connection with the earlier paper on double bands (Newman, '15). I know of no method for presentation of data of this kind that is at once so intelligible and so compact as the pictorial diagram used in this and the former paper. When one has read the key to the table there should be no difficulty in understanding the data thus presented. The facts are first presented for those sets in which both mothers and offspring have double scutes, covering pages 182 to 188, and there follows as an appendix to this paper a table for those sets in which the mother was without double scutes, but in which one or more of the offspring have inherited the double scutes from the unknown father. See pp. 204 to 207.

KEY TO TABULATION OF DOUBLE SCUTES.

Each solid block of bands shows the anomalies in position as though the bands were straightened and placed with the right-hand end to the right and left-hand to the left. The number of the set with the sex of the quadruplets is indicated above and at the left of each block. Bands of the mother that show anomalies are marked *M*; those of the offspring that show anomalies are marked according to previous custom I., II., III., IV. I. and II. are a natural pair, II. being a primary bud individual and I. its twin secondary bud derivative. Similarly III. and IV. are a natural pair, IV. primary and III. secondary. If the anomaly occurs in different bands of the same individual a bracket includes the Roman numerals indicating the individual fetus concerned. The various types of double scute are drawn in upon the band in as

nearly as possible the position in which they occupy, but they take up more space laterally than is actually the case. In addition to positional location the number of each scute, counting from either of the margins or from the middle, is given by an arabic numeral upon the pictured scute, the direction from which the count has proceeded being indicated by an arrow unless this is too obvious to need indication. The arithmetical middle of a band is indicated by a dotted vertical line, except in a few cases where the right and left halves of two different bands of a single individual are placed in the same line, in which case a solid line is used to separate these heterogeneous half bands. This change of method may be a little confusing at first, but it was introduced to save space. The band in which the anomaly occurs is numbered with an arabic numeral followed by a colon and a figure indicating the total number of scutes in that band. For instance 6 : 63 means band 6 which has a total of 63 scutes, counting the double scute as two scutes. L.S. refers to the last scapular row of scutes, next to the bands. This mode of tabulation admits of a very condensed record of a large amount of data.

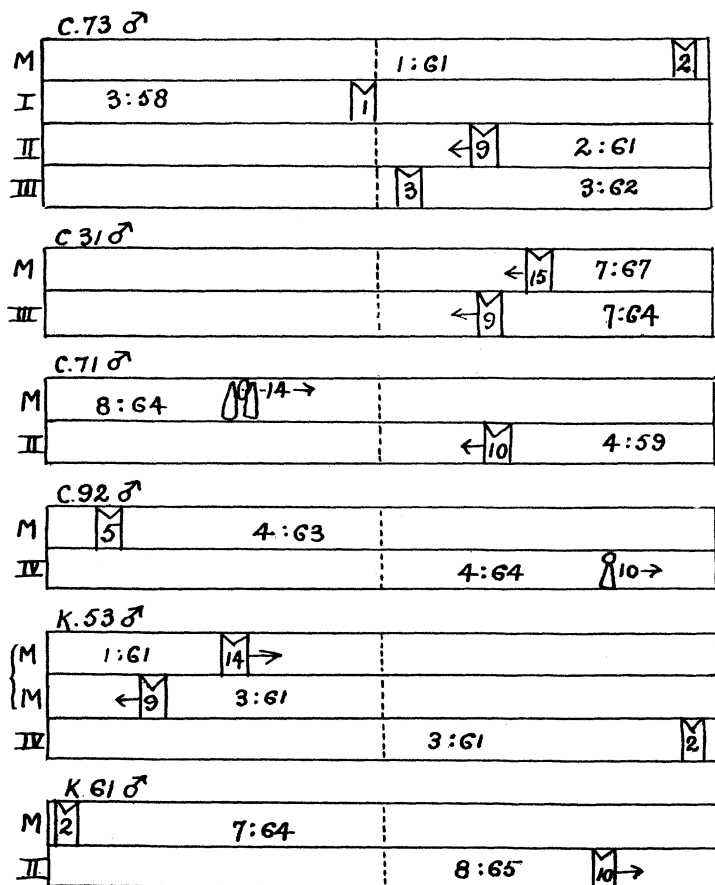


FIG. 9.

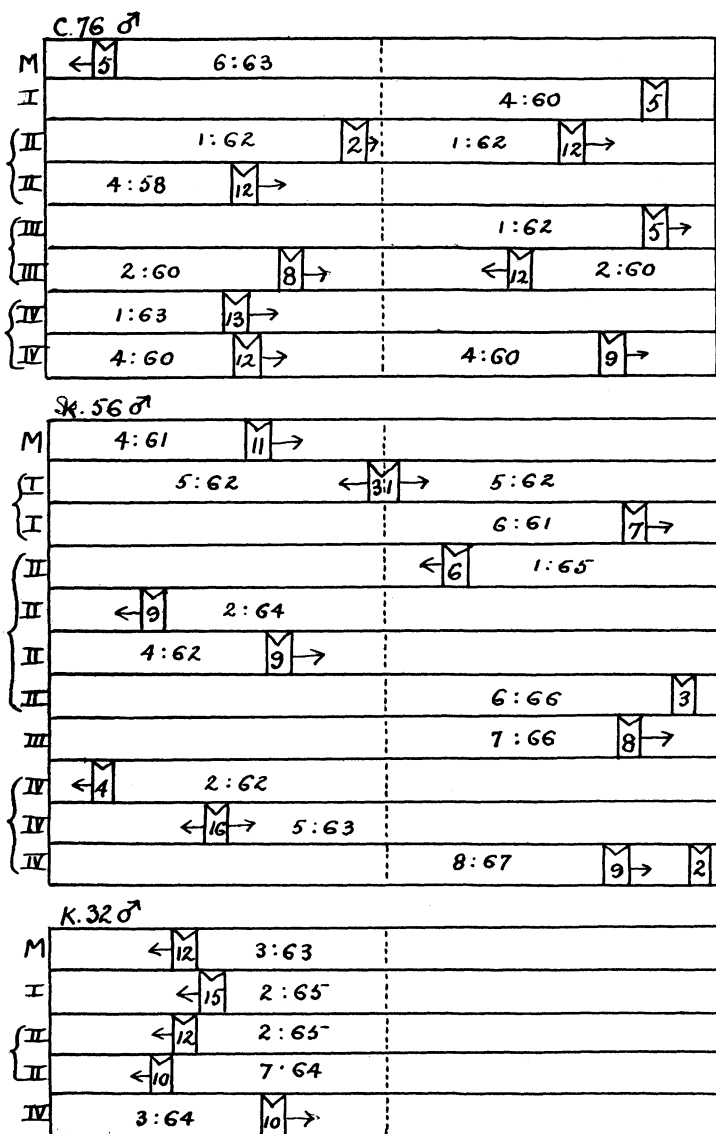


FIG. 10.

K. 76 ♂

M	3	8:66	← 8	2:63
I	9:66	12 →	← 6	3:62
II	1:64	2	← 8	4:62
II			8:64	← 18 →
III			8:67	3
IV	← 12	8:67	← 11	5:62

K. 70 ♂

M			← 6	2:58
M			← 6	3:58
I	3	4:58		1:57
I	3	6:60		7:59
II	← 8	1:57		
III				7:62
IV			← 6	2:57
V				6:60

C. 30 ♂

M				1:61	2
M				7:63	7 →
I				1:60	3
II	2	1:61			
III	2	1:61		2:60	2
IV	2	1:60		2:61	2

K. 25 ♂

M			← 6	2:58
I	← 7	1:58		
II			1	7:60
IV				6:61

FIG. II.

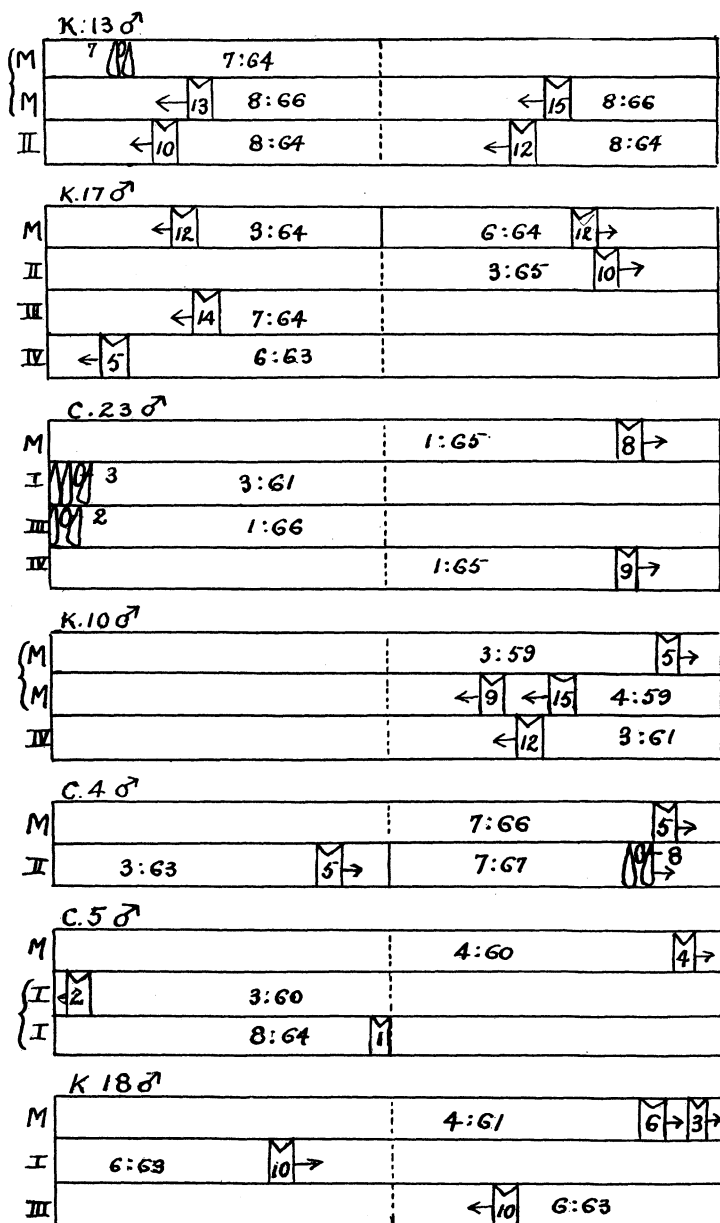


FIG. 12.

K.5 ♀

M		8:67	← 15
I	← 4	6:63	
I	← 10	8:63	
II		1:63	9 →
III	8:65	2	
IV	← 9	1:61	1:61 2
IV	3:60	5 →	7:62 13

C.24 ♀

M		1:62	4
I	3	7:63	9:65 9 →
II	3	1:64	
II	← 10	7:65	
III	← 5	3:58	
IV	4	1:61	

K.48 ♀

M	4:64	13 →	2:63	2
M	2	8:67		
III	10-3	2:63		
IV	4:61	9 →		

K62 ♀

M	← 15 →	4:60	2:64	14 →
I	10-2	1:61		
I		3:59	← 30 →	3:59
III			1:62	10 →
IV	← 15 →	4:61	2:58	8 →

K.45 ♀

M	10-3	2:57		
II			8:66	10 →

C65 ♀

M	2		1:62	
II	2		L5:60	

FIG. 13.

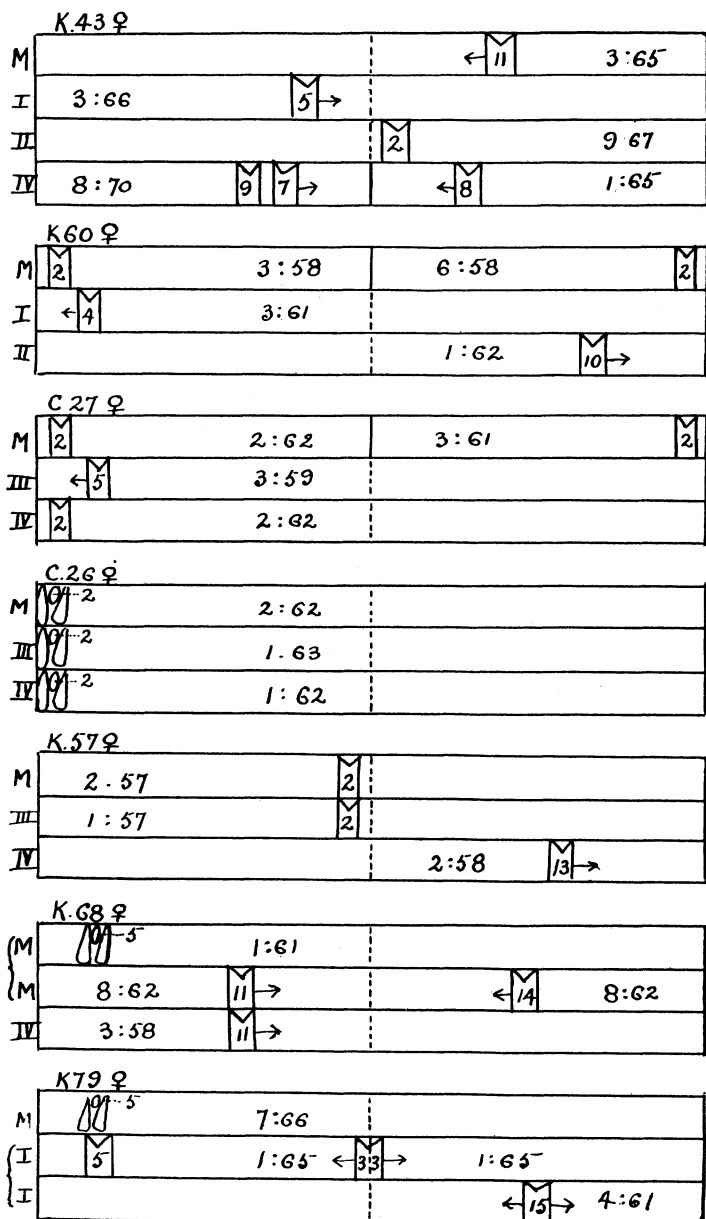


FIG. 14.

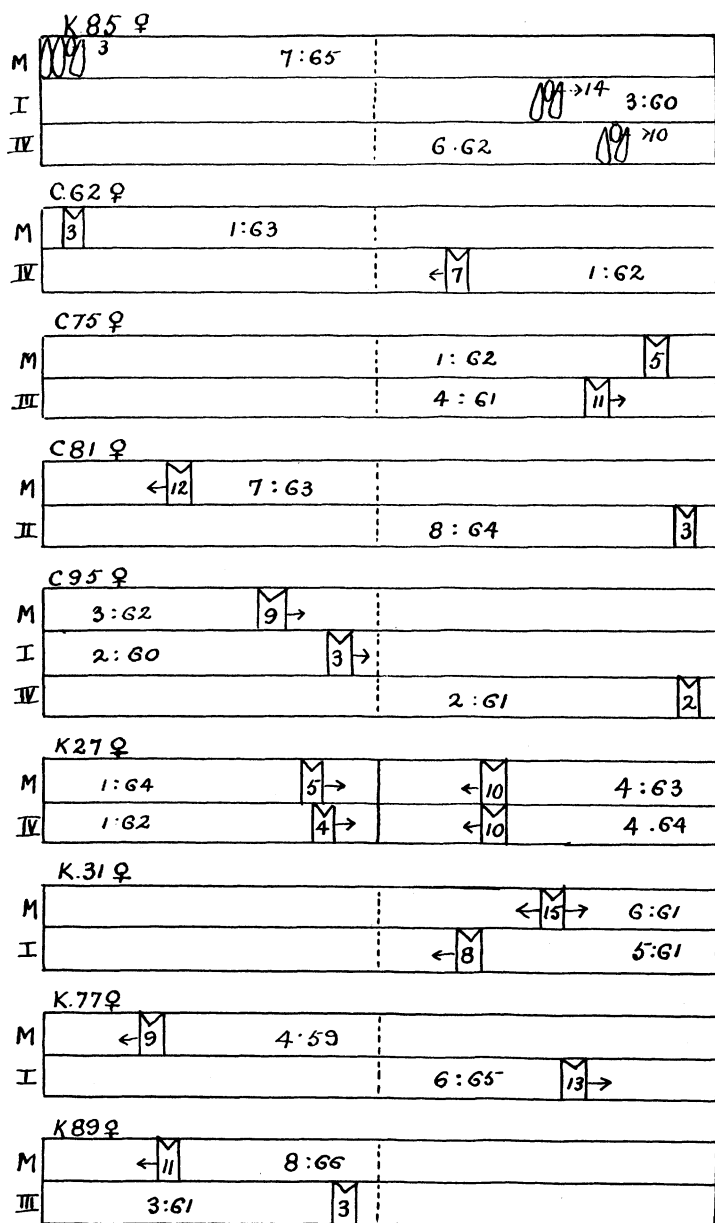


FIG. 15.

1. *The Difficulties in the Way of Accurately Analyzing the Data.*

It would be interesting to analyze the data given in the tabulation above, but before an intelligent analysis can be made some of the chief sources of error should be pointed out.

1. Perhaps the most obvious hindrance to accurate analysis of the data appears in the fact that we cannot be certain, if more than one anomaly appears, that the inheritance is solely from the mother, for there must obviously be a fairly large number of sets of quadruplets in which both parents had anomalies. Some sets show clearly this biparental influence, but in many cases it is impossible to decide whether the condition is inherited from the mother alone or is of biparental origin.

2. Another source of error in presenting a pictorial tabulation of the localization of these minute elements is the result of a somewhat arbitrary method of determining the middle of a band, for although I have chosen to locate the middle by dividing the scutes into equal numbers on right and left sides, I feel sure that the arithmetical middle does not always correspond to the morphological middle. There are definite indications in many cases that there are more scutes on one side of the median dorsal line than on the other, in which instances the arithmetical middle is obviously not median. This condition is probably due to the fact that when two parents with decidedly different scute counts mate we may get the maternal number in one half band and the paternal in the other. The middle point therefore is not a very favorable landmark for scute localization but it seems necessary to use it in order to indicate unilateral symmetry reversals. Localization from the lateral margins of the bands is much safer than localization from the middle and it is quite obvious that laterally placed scutes show much closer correspondence in position than do those near the middle.

3. Another factor that shows the inadequacy of the numerical localization method inheres in the fact that different bands vary greatly in number of scutes, ranging from 57 to 70 in the present collection. Now a scute that is pictured as being 5 scutes from the margin in a band of 57 scutes is morphologically farther from the margin than a scute located 5 places from the margin of a band of 70 scutes. So when we are comparing the locality of the

scutes of one individual with another we should bear in mind the numbers of scutes in the various bands dealt with.

2. *Classification of Types of Inheritance and Resemblance among Quadruplets.*

Analysis of the individual cases reveals several well-marked categories:

- (A) Strikingly close resemblances between mother and offspring, or among the different fetuses of a set.
- (B) Cases of symmetry reversal between parent and offspring.
- (C) Cases of mirror-imaging among the fetuses of a set.
- (D) Cases of half-band reversals of symmetry between mothers and offspring.
- (E) Cases of half-band reversals between different fetuses of a set.
- (F) Cases of half-band reversals in the same individual.
- (G) Longitudinal reduplications down the long axis.
- (H) Transverse reduplications in a single band.

Each of the categories will herewith receive separate attention.

A. Strikingly Close Resemblances between Mother and Offspring, or Between the Different Fetuses of a Set.—Cases are here dealt with in which the form of the anomaly, its localization and symmetrical relations are the same, or very nearly so, in two or more members of a set, the mother included. The most striking cases are considered first.

Set *K* 27 (p. 189) shows the most remarkable case of exact resemblance. The mother has two double scutes in two different bands, and one of the offspring (fetus 1) has the same double scutes in the same positions of the same two bands as in the mother. Here we have a little difficulty due to locating the morphological middle of the first band. If we take the arithmetical middle, as has been done, the double scute of band 1 of the mother is five scutes from the middle, but that of fetus 1. is four scutes from the middle. If we count from the margin, however, the scute is number 28 from the left in both cases, for there are two more scutes to the band in the mother than in the offspring.

Set *C* 26 (p. 188). The mother has a small scute (like Fig. 2*a*) in band 2, two places from the left hand margin. Fetuses II. and IV. (one of each pair) have identical anomalies but shifted to band 1.

Set *K* 57 (p. 188). The mother has scute 2 from the middle of band 2 double, and fetus III. has an identical anomaly in band 1.

Set *C* 30 (p. 185). The mother has a double scute in band 1 situated two places from the right-hand margin. Fetuses III. and IV. have in band 2 an anomalous scute (like Fig. 2*a*) two places from the right-hand margin. These two elements have bilaterally symmetrical equivalents on the left hand side of band 1.

Set *K* 70 (p. 185). The mother has in band 2 a double scute 6 places to the right of the middle. Fetus IV. has an exactly equivalent anomaly.

Set *C* 76 (p. 184). Fetus II. has in band 4 a double scute 12 places to the left of the middle. Fetus IV. has an exactly equivalent element.

B. Cases of Symmetry Reversal between Mother and Offspring.—All cases are to be included here in which an anomaly of the mother is repeated in the offspring but on the opposite half of the carapace.

Set *C* 76 (p. 184). Mother has in band 8 a double scute three places from the *left* margin. Fetus III. has in band 8 a double scute 3 places from the *right* margin.

Set *C* 30 (p. 185). Mother has a double scute 2 places from the *right* margin of band 1. Fetuses II., III. and IV. each have an anomalous element (like Fig. 2*a*) two places from the *left* margin of band 1.

Set *C* 24 (p. 187). Mother has in band 1 a double scute 4 places from the *right* margin. Fetus IV. has in band 1 a similar element 4 places from the *left* margin. Fetus II. has in band 1 a similar element 3 places from the *left*, and fetus III. has in band 3 a similar element 5 places from the *left*. We have here several degrees of exactness in the mirror-imaging of the inherited anomaly.

C. Cases of Mirror-Imaging among the Fetuses of a Set.—Set *K* 70 (p. 185). Fetus I. has a double scute 3 places from the

left margin of band 6, and fetus III. has a similar element 3 places from the *right* of band 7. Note that these fetuses are not pairs but face each other from opposite sides of the vesicle. Both are secondary bud individuals.

Set *C* 30 (p. 185). Fetuses I. and II., a pair, have striking mirror-image resemblance. Fetuses III. and IV., the other pair, have the same anomalous element bilaterally.

Set *C* 76 (p. 184). Fetus III. has a double scute 12 places to the *right* of the middle of band 2. Fetuses II. and IV. each have identical elements on the *left* side.

Set *K* 18 (p. 186). Fetus I. has a double scute 10 places to the left of the middle of band 6. Fetus III., which faces I. across the vesicle, has a similar element 10 places to the *right* of the middle of band 6.

D. Cases of Half-Band Reversals of Symmetry between Mother and Offspring.—In this group are included cases in which the parent and offspring have the anomaly confined to the same, right or left, half of the carapace, but the symmetry of that half of one is the mirror-image of the same half of the other.

Set *K* 70 (p. 185). Mother has a double scute 6 places to the *right* of the *middle* of band 2. Fetus I. has a double scute 6 places from the *right hand margin* of band 1. If this band had been arranged so that the right hand half were simply shifted over to the left side it would have been an ordinary case of mirror-imaging.

Set *K* 25 (p. 185). Mother has a double scute 6 places to the *right* of the *middle* of band 2. Fetus I. has a similar element 7 places from the *left hand margin* of band 1. This is a case of a double reversal. Turn either of these half bands end for end and an ordinary mirror-image case would result.

Set *C* 4 (p. 186). Mother has a double scute 5 places from the *right margin* of band 7. Fetus II. has a similar element 5 places to the *left* of the *middle* of band 3, which is evidently the reversed mirror-image of a similar element in band 7 of the same fetus situated 8 places from the *right-hand margin*.

E. Cases of Half-Band Reversals between Different Fetuses of a Set.—These are cases strikingly like the unilateral reversals of finger-print patterns described by Wilder for duplicate human twins.

Set K 76 (p. 185). Fetus II. has a double scute 12 places from the *right margin* of band 1. Fetus II. has a similar element 12 places to the *right* of the *middle* of band 1. Again fetus III. has a double scute 8 places to the *right* of *middle* of band 2, and fetus IV. has a similar element 9 places from the *right margin* of band 4. Here each pair of fetuses mirrors the other as to the right half of the carapace.

Set K 56 (p. 184). Fetus I. has a double scute 7 places from the *right margin* of band 6. Fetus II. has a similar anomaly 6 places to the right of the middle of band 1 and a second anomaly 9 places from the *left margin* of band 2, and a third anomaly 9 places to the *left* of the *middle* of band 4. Fetus III. has a double element 8 places from the *right margin* of band 7. Fetus IV. has a similar element 4 places from the *left margin* of band 2 and another element 9 places from the right margin of band 8. All of these anomalies are, I believe, directly inherited from the mother, who has a double scute 11 places to the *left of the middle* of band 4, but there are numerous reversals within the set involving a shifting up and down the long axis. This is one of the most complex cases in the collection and would bear careful study as it illustrates most of the symmetry phases seen in armadillo quadruplets.

F. Cases of Half-Band Reversals in the Same Individual.—Set K 56 (p. 184). Bands 2 and 4 of fetus II. have a reversed symmetry of the left half.

Set K 76 (p. 185). Fetus II. has a reversed symmetry in bands 1 and 4; Fetus IV. has a reversed symmetry in the two halves of band 4.

G. Longitudinal Reduplication Down the Long Axis.—It is fairly common to find an inherited anomaly appearing not merely once but repeated in two or more bands. Sometimes an anomaly of an anterior band is balanced by a similarly located anomaly in a posterior band. The condition is somewhat like that which appears in transverse rows of double scutes that are called double bands, but the tendency for an extended condition of the anomaly is vertical instead of horizontal and is seldom continuous.

Set K 32 (p. 184). Fetus II. has a double scute in band 2 and another exactly in a vertical line with it in band 7.

Set *K* 70 (p. 185). Mother has scute 6 to right of middle double in bands 2 and 3. Fetus I. has scute 3 from the left margin double in both bands 4 and 6, also in bands 1 and 7. Fetus IV. has in bands 2 and 6 the same double scutes as fetus I. has in bands 1 and 7, but there is a symmetry reversal in the half bands. There seems to be a strong tendency for the offspring in this set to inherit the vertical reduplication of the mother.

H. Transverse Reduplication in a Single Band.—Here are included cases in which two or more double scutes occur close together but not contiguous in the same band. Such cases are probably in the nature of interrupted band anomalies. Examples may be seen in sets *K* 18, *K* 10, *K* 43, *K* 56. There are as many more cases in sets with normal mothers that are shown in the appendix.

The interpretations offered in the above analysis may be open to objection in certain cases but there can be no controversy as to the nature of the great majority of cases. There is strong evidence of much mirror-imaging between pairs and between individuals of a pair and there are numerous cases of half-band reversals quite like those occasional reversals of finger-print patterns described for duplicate human twins by Wilder, and which Bateson believes to be evidences of a former system of symmetry common to the two individuals before the separation of their primordia. If these rare and vestigial reversals in duplicate human twins are to receive the above interpretation, we should feel no hesitancy about a similar interpretation of the quite frequent occurrence of symmetry reversals in armadillo quadruplets.

C. DISCUSSION AND CONCLUSIONS.

1. *The Problems of Inheritance and Segregation.*

(a) *The Exceptional and Unique Character of the Material.*—No other animal that I know of is so beautifully adapted for the study of specific and individual variability as is the armadillo. The strikingly diagrammatic arrangement of the integument into the five armor shields furnishes an unusual opportunity for accurate enumeration of units and for a study of inter- and intra-individual correlation. These characters, moreover, are

definite in numbers and arrangement long before birth. How fortunate a circumstance it is that this species, which is unique in its polyembryonic method of reproduction, should at the same time be unique in its possibilities for biometric treatment! I was especially impressed with this fact lately when I tried to get some basis for a comparison between cattle twins and could find nothing satisfactory for the purpose. The same would be true for sheep, cats or any other mammal. Differences in size, the only measurable differences in these species, are quite unsafe criteria for the determination of coefficients of correlation, since they are notoriously affected by differences in nutrition. Although any part of the integument of the armadillo is superior for the establishment of correlation constants to anything found in any other mammal, the banded region, on account of its regularity, definiteness and specific fixity, is preeminently adapted for the study of inheritance and of the degrees of resemblance and difference among individuals of a polyembryonic set.

So regular is the banding that it would be impossible to discover any symmetry in the bilateral arrangement of integumentary structures were it not for the occurrence of occasional band irregularities (double bands) and of fairly frequent double scutes. These peculiarities of the integument furnish landmarks for the study of symmetry relations that are quite uniquely suitable for such studies and are more readily comparable than are the fingerprint patterns of human duplicate twins that have been used for a similar type of study.

(b) *Irregularities in the Inheritance of Band and Scute Anomalies.*—That band and scute anomalies are definitely inherited is proven by the fact that anomalies are always present in offspring of mothers that show the anomaly. The real problem is to explain why all four features of a set of quadruplets do not inherit these anomalies equally and in the same form. Since they come from a single fertilized egg they have the same genetic constitution and should be identical unless there exist certain agencies that result in an irregular distribution of the differentiating factor responsible for anomalies. That these agencies which produce irregular distribution of anomalies among the individuals of a set are not environmental is certain, for there appears to be no

environmental inequality except that of nourishment, and differences in nourishment so great as to strikingly affect the size of the individuals do not at all affect the inheritance of anomalies. This could be readily shown by a comparison of sets that show marked size inequality with sets that show size identity.

If then the agency at the basis of irregular distribution of anomaly factors is not environmental, it must be some sort of internal agency. I have been unable to think of any mechanism engaged in either regular or irregular distribution of inheritance factors except the obvious mechanism of mitotic cell division. If this mechanism worked in a perfectly accurate and equitable fashion there would be no opportunity for any irregularities in the distribution of differentiating factors; but there are irregularities and hence the mechanism must lack accuracy.

If the factor or factors for anomalies are present in the oöperm, as we are forced to believe, they must have their seat either in the nucleus or in the cytoplasm. Since the anomalies are evidently as strongly inherited from the father as from the mother, it is hardly likely that the locus of the factors is cytoplasmic, for the male cell has an insignificant cytoplasmic organization. In view of these facts we may safely assume that the locus of the factor is in one or more chromosomes. When all four fetuses inherit an anomaly, we must assume that the factor has been equally distributed to the daughter cells of the first cleavage and probably for several successive cleavages. If, however, the anomaly is confined to a pair of embryos derived from one half of the vesicle, it seems likely that the factor was so distributed as to be totally absent from one of the first two blastomeres. When only one embryo inherits the anomaly the unequal distribution may have occurred during the second or later cleavages.

After a long search for some more satisfactory explanation of the facts than that afforded by a resort to the mechanism involved in cleavage, I have been finally driven back upon this explanation by the facts immediately to be brought out in connection with the phenomenon of somatic and germinal segregation.

(c) *Somatic and Germinal Segregation*.—The particular method of polyembryonic reproduction in the armadillo is definitely

known to be a process involving a precocious dichotomous budding initiated by the primitive ectoderm. The individual fetuses are produced agamically as bud products and therefore constitute a clone; so whatever somatic variations occur among the four fetuses of a set are obviously types of clonal variation.

Bud or clonal variations have for a long time been propagated vegetatively by cutting, grafts, etc., and are known to hold true to their somatic characters. The explanation of bud or clonal variations that has usually been offered involves the introduction of two causal factors, one internal and the other external. It is said that a local peculiarity may be induced by local conditions outside of the bud tissue itself, such as unfavorable or extra favorable position on the plant; but such an explanation involves many theoretical difficulties. A more acceptable explanation involves the assumption that there is some segregative mechanism that brings about an uneven distribution of inherited factors, so that one type of factor may be present in one part of the growing plant and absent in another. Special cases of somatic segregation are those cases that we have been accustomed to consider under the term *particulate* or *mosaic* inheritance. Such inheritance conditions are supposed to be due to a segregation in a single hybrid offspring of the opposed characters of the two parents. When, for example, a cross is made between a plant with white and one with red petals, we may get a hybrid possessing flowers with some white and some red petals. This is said to be a result of the segregation of parental color factors so that some cells get certain factors and others do not.

So far as I am aware it has not been shown whether in bud or clonal variations, germinal segregation goes hand in hand with somatic segregation. If a green plant that produces a white bud variation should be found to produce flowers on this bud that bred true to the white character, we would have a very clear case of parallel somatic and germinal variation.

Now in the armadillo we have precisely this state of affairs, as can be brought out by a study of the inheritance of double bands and double scutes. For, when some of the fetuses of a set exhibit the anomaly as shown in the mother and others do not, we have unequivocal somatic segregation; but we have

something more than this, since those individuals that have the inherited anomaly in the soma also must have the factor for the anomaly in the germ plasm, else how can we account for the fact that whenever a mother has an anomaly it appears in one or more of her offspring?

This segregation must have occurred at a period prior to the separation of primary germ layers, in order to account for the strict parallelism between the germinal and somatic cells, and I have reason to look back to the earliest cleavage divisions as the probable time and occasion of the segregation of determinative factors. This view is arrived at after considering all of the available facts and I believe is justified. Strangely enough we seem once more to be driven back to the cleavage stages for an explanation of the phenomena of twinning, but there is a vast difference between merely assuming the blastotomy origin of twins and accepting the cleavage mechanism as the most probable apparatus responsible for parallel germinal and somatic segregation of inherited factors.

Moreover segregation of inherited anomalies among individuals of polyembryonic sets is one problem, while the symmetric or asymmetric localization of these factors in the soma of the individual is another—the problem of organic symmetry.

2. *The Peculiar Symmetry Relations Among Quadruplets.*

(a) *Normal and Reversed Symmetry in the Occurrence of Anomalies and their Significance.*—If no complicating factors entered into the matter of the inheritance of double bands or double scutes, we would expect to find a double scute of the left margin of a given band in the mother inherited as a similarly located double scute by all four offspring. We have attempted to explain the failure of the anomaly to appear in all of the offspring of a litter by positing a segregative mechanism operating during cleavage. Such a mechanism, however, appears inadequate to explain the symmetry relations so peculiar to polyembryonic reproduction.

The mirror-image type of symmetry is normal for the antimeric halves of a single individual and exceptions to or breaches of the mirror-image type of symmetry affords a new problem. Double

monsters are also frequently characterized by mirror-image symmetry, due to the fact that the two halves are not physiologically isolated and are therefore parts of a single system of symmetry.

Occasional vestiges of mirror-imaging have been described by Wilder for the finger-print patterns of duplicate human twins, as when the pattern of the right index finger of twin *A* is the mirror-image of the left index finger of twin *B*. These symmetry reversals in duplicate twins have been emphasized as evidences of the monovic origin of such individuals and the reversals themselves have been interpreted as the last trace of an early symmetry formerly common to the two individuals but subsequently largely outgrown.

Now in the armadillo there are many definite evidences of a system of symmetry common to all of the quadruplets, upon which has been superimposed a secondary symmetry system between twins. This in turn is more or less completely obliterated later by a tertiary symmetry between the antimeric halves of the single individuals. In some sets evident traces of the primary system of symmetry persist as mirror-image relations between individuals of opposite pairs, but it is more usual to find no trace of the primary system. The secondary mirror-imaging between pairs is far more commonly in evidence, but is frequently obliterated by the tertiary mirror-imaging between antimeric halves of the same individual, which latter is the prevailing symmetry system. An analysis of this intricate interplay of three grades of symmetry systems is by no means a simple task, but in the foregoing descriptions of individual sets we have indicated our interpretation of the various mirror-image and symmetry reversal phenomena that form the basis of such an analysis. In general, mirror-imaging between individuals of opposite pairs is interpreted as an evidence of the early system of symmetry present in the embryonic vesicle before polyembryonic budding began. When the primary buds are formed they are the product of the antimeric halves of the undivided embryo and therefore should have mirror-image relations, but a partial physiological isolation of the two buds permits a certain degree of reorganization or regulation in the symmetry relations, that tends partially

to obliterate the original symmetry relations of the undivided embryo. Similarly, when each primary bud subdivides to form the secondary buds that are the primordia of the definitive individuals, a certain residuum of the primary bud symmetry system is carried over, manifesting itself in mirror-imaging between the twins derived from the same primary bud. But here again a certain amount of regulation occurs so that a third system of symmetry, the bilateral symmetry of each individual, tends to obliterate former systems of symmetry.

A further evidence of the existence of a primary system of symmetry relations is seen in the mode of formation of the secondary buds. Each primary bud gives off to its *left* a secondary bud as though the whole vesicle had a growth whirl to the left. It appears to be acting as a single system at the very time when polyembryonic processes are most active.

(b) *The Closer Symmetry of Pairs and its Significance.*—One of the most striking early discoveries resulting from a study of armadillo quadruplets was that the four fetuses of a set are paired so that one pair is fixed to the right-hand placental disc and the other pair to the left-hand placental disc. These discs lie respectively on the right- and left-hand sides of the uterus. The pairs are more strikingly identical than are the quadruplets as a whole and they more often exhibit interindividual mirror-imaging than do the individuals of opposite sides of the vesicle. It at first seemed probable that this condition was due to the "fact," carried over from the literature on the origin of human duplicate twins, that one pair was derived from one and the other from the second blastomere of the two-cell stage. Now that we know more about the embryonic history of the armadillo we are less inclined to relate the symmetry of the vesicle to the symmetry of the oöperm.

It will be recalled that the early blastodermic vesicle, when it becomes fixed to the mucosa of the fundus uteri, adheres by means of a predetermined disc of cells called the "Träger." This disc is evidently derived from the animal pole of the egg and hence we have a mechanism for fixing the principal axis of the embryo and causing it to coincide with that of the mother. The blastodermic vesicle, even if it had a predetermined bilaterality, could

hardly fix itself so that its dorso-ventral axis would correspond with that of the uterus, so we are driven to the conclusion that the embryo at the time of fixation has no bilaterality, but acquires its bilaterality from that of the mother. The first indication of bilaterality is seen when the vesicle elongates toward the right and left oviducal openings of the uterus and when bilateral buds of ectoderm grow out to the right and left sides. In other words the bilaterally symmetrical arrangement of the embryonic primordia is imposed upon the vesicle by the form of the uterus.

These first embryonic buds, the primary buds, stand for two pairs of twins, each bud redividing to form two secondary buds, each of the latter going to form a separate embryo. The closer resemblance between the twins of one side is simply the expected result of their community of origin, for they are the product of the longitudinal splitting of a single primary bud of ectoderm. In other words both have been derived from a rather limited area of cells which is separated from the primordia of the opposite pair by a considerable zone of extra-embryonic tissue. On any theory of unequal distribution during cleavage of differentiating factors we would expect these twin products of the horizontal splitting of a common primordium to be closely similar to each other and to show a relatively large amount of mirror-imaging.

(c) *Bateson's Views Concerning Twinning*.—In his book "Problems of Genetics" Bateson has an interesting and suggestive chapter on "meristic phenomena" in which he lays great stress upon the fundamental importance of the problem of cell division and other division phenomena. He conceives of the phenomena of bodily symmetry as a direct result of the symmetrical features of cell division. Twinning in mammals is for him a special case of the effects of cell division for he adopts the traditional view that the twins result from a physiological isolation of the blastomeres of the two-cell stage of cleavage. Bateson accepts Wilder's position that duplicate twins are in a series with double monsters of various grades. Double monsters show all degrees of mirror-imaging, while duplicate twins show only vestiges of this phenomenon. Much emphasis is laid upon the few cases of reversed finger-print patterns in the duplicate twins described by Wilder. Any sort of mirror-imaging (symmetry reversal) is an indication

of a system of symmetry common to both individuals, whether they are joined or separate.

In closing it may be of interest to state that an examination of a considerable number of sets of quadruplets reveals no indication of a reversal of symmetry in the viscera. As in human duplicate twins symmetry reversals are confined to the integumentary structures. Why should this be so? Bateson propounds this inquiry for duplicate twins as follows: "If anyone could show how it is that neither of a pair has transposition of the viscera the whole mystery of division would, I expect, be greatly illuminated." Now in the armadillo the process of polyembryonic budding that results in twinning is initiated and carried out in the ectoderm, while the endoderm becomes involved only passively and considerably later. Here we probably have the answer to Bateson's inquiry, for symmetry reversals involve only the tissues that are primarily concerned in twinning. How much this statement serves to illuminate the mystery of division I am not prepared to say.

I am inclined to believe that duplicate human twins become physiologically isolated at a considerably earlier period than do armadillo quadruplets, and my reason for this belief is founded on the fact that there is so very little mirror-imaging in the former and so much in the latter. It appears to be a good general rule that the earlier the separation the more complete is the reorganization of symmetry relations in the separated individuals and the less residuum of the original common symmetry. Double monsters doubtless begin to separate comparatively late in ontogeny and hence show very pronounced mirror-imaging. Armadillo quadruplets appear to exhibit a condition intermediate between duplicate twins and double monsters for they have an interesting combination of the effects of an original common system of symmetry and of secondary and tertiary systems of symmetry. Since it seems entirely probable that human duplicate twins are separated at a much earlier period than are armadillo quadruplets, it may not be unreasonable to look for this separation at some period of cleavage. Or there may be a division of the inner cell mass into the primordia of two embryos. The problem of the exact mode of origin of duplicate human twins is however likely to remain unsolved for a long time to come.

APPENDIX.

Sets of Quadruplets Inheriting Double Scutes from Unknown Fathers.

Purely as a matter of record there is included herewith as an appendix a pictorial tabulation of 31 sets of fetuses from normal mothers but themselves with anomalies. There is every reason to believe that these characters have been inherited from the unknown fathers. There are 15 female sets and 16 male sets. The same plan of representing the occurrence and location of these double elements is followed as was used in the earlier tabulation, the key to which is given on page 181.

Since all of these cases are uniparental while many of the cases discussed earlier are biparental, one would expect a simpler state of affairs and fewer double scutes per set. This is actually the case. The interrelations between the different fetuses of a set are on the average much more clearly defined since there is no confusing admixture of elements from both parents. These facts go far to prove that the conclusions reached in the earlier part of the paper regarding modes of inheritance are well founded.

Many striking cases are seen of close resemblance between twins, of mirror-imaging and half-band reversals between twins, all of which reinforce the conclusions reached on the basis of the data heretofore discussed. Nothing, however, would be gained by calling further attention to individual cases. The interested reader will be able to pick out and classify for himself the various types of anomaly. The pictorial method of recording these elements may need a little study on the part of the reader but is fully justified by the fact that a large amount of valuable data, the like of which may never again be available, is given in very compact form.

Correction.—On page 27 of the first installment of this study (Newman '15) is figured the double band arrangement in set *K 2*. This set was classed erroneously among sets the mother of which had no anomalies. The notebook in which the data was taken shows the mother of *K 2* was misplaced and later found and has two anomalies. Band 3, which has 64 scutes, has a double scute, like Fig. 2*a*, 16 places to the right of the middle. Band 5 (63

K 49 ♂		
II	2:63	M 3
IV	← M 4	1:66
IV	9:65	← M 13
K 81 ♂		
II	← M 11	6:63
IV	4:65	M 10 →
C 28 ♂		
IV	13 ← M 10	1:64
IV	6:65	M 13 →
K 39 ♂		
I	M 3	6:61
II	3:60	← M 10
K 58 ♂		
I	M 3	7:61
II	3:58	M 1
K 81 ♂		
II	← M 11	6:63
IV	7:65	M 10 →
K 24 ♂		
III	4:60	← M 11
IV	2:60	M 15 →
K 21 ♂		
I	5:59	← M 4
II	← M 9	1:61
K 54 ♂		
III	← M 15	1:65
K 83 ♂		
IV	M 12 →	9:64

FIG. 16.

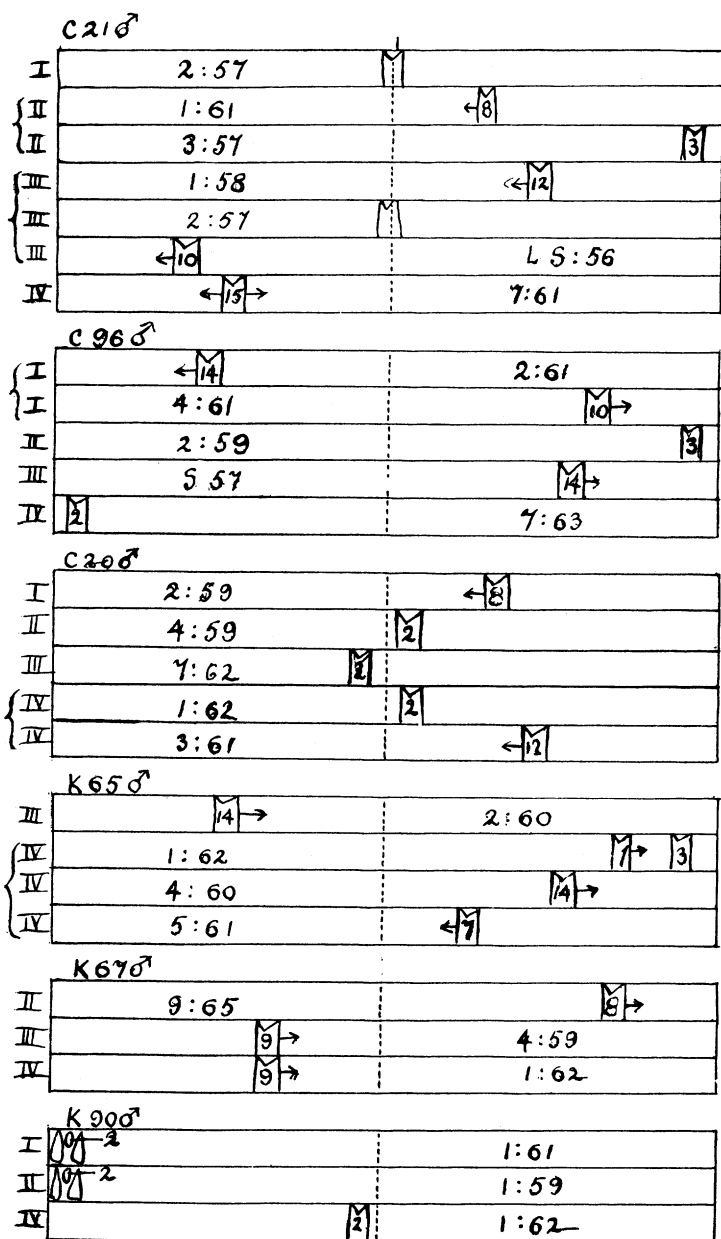


FIG. 17.

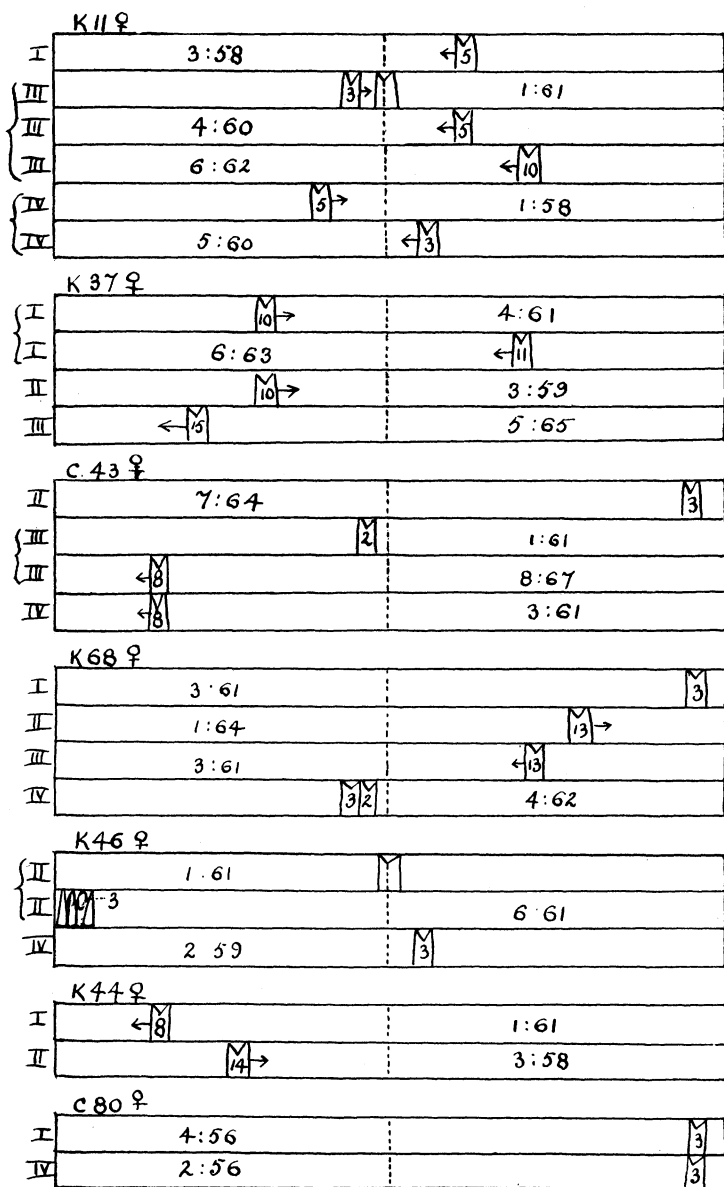


FIG. 18.

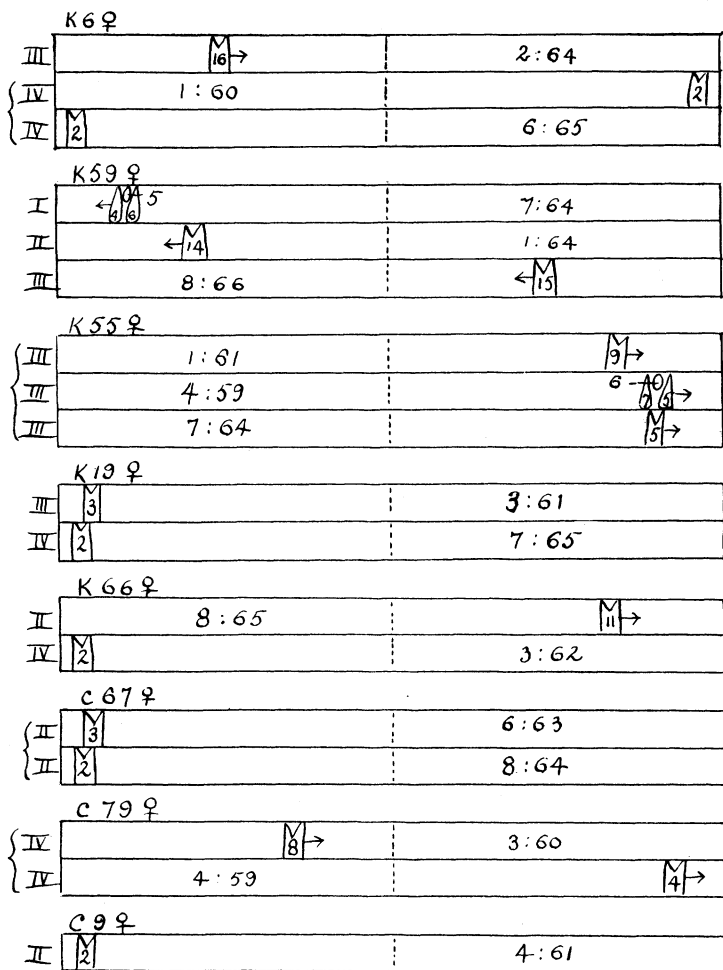


FIG. 19.

scutes) has a double scute 5 places from the right-hand margin. These two anomalies mark about the inner and outer limits of the band doublings seen in the offspring. This set shows almost perfect mirror-imaging of the whole set of quadruplets. The two primary bud fetuses II. and IV. mirror each other since both have the anomaly bilaterally; the two secondary fetuses I. and III. are also mirror-images, III. having the anomaly on the right and I. on the left. All of these anomalies occur in band 1.

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